SEASONAL CHANGES IN THE COMMUNITY STRUCTURE OF THE MACROBENTHOS INHABITING THE INTERTIDAL SAND AND MUD FLATS OF BARNSTABLE HARBOR, MASSACHUSETTS

ROBERT B. WHITLATCH [1]

The University of Chicago, Committee on Evolutionary Biology, Chicago, Illinois; and Marine Biological Laboratory, Woods Hole, Massachusetts

Since the pioneering works of Peterson (1918) and Thorson (1957), most of the attention of workers in the field of marine benthic ecology has been directed to short-term sampling surveys of particular environments in an attempt to delimit given macrobenthic species assemblages or communities. These investigations have generally concluded that given species assemblages are greatly influenced by sedimentary parameters (*e.g.,* grain size), and that the communities are not tightly functioning units but rather are composed of individualistically distributed species which respond to a complex set of environmental and biological parameters. The result of such findings is that given particular sedimentary parameters, *a posteriori* predictions of what faunal assemblages will occur at a particular site are possible. However, over longer periods of time, the predictive value of determining the distribution of given species groupings is greatly reduced. Any naturally occurring community of organisms is not only distributed in space but also in time. To better understand patterns of community organization, therefore, more long-term studies are needed to provide basic information regarding temporal community structure and to elucidate those factors affecting species compositional change.

Studies on temporal changes in community structure and species composition are not common. Of these studies (*e.g.,* Sanders, 1960; Pearson, 1971, Tenore, 1972; Lie and Evans, 1973; Watling, 1975; Levings, 1975), most are concerned with subtidal environments. Surprisingly, there are fewer studies dealing with time-related community changes in intertidal environments (*e.g.,* Bloom, Simon and Hunter, 1972; Johnson, 1970; Holland and Polgar, 1976). Intertidal environments provide an excellent opportunity to study the effects of seasonal change, since physical variables fluctuate with greater amplitude than in bordering subtidal habitats, thus subjecting organisms inhabiting them to greater amounts of stress.

The purpose of this study is to describe the general macrobenthic community structure of a portion of the intertidal sand and mud flats of Barnstable Harbor, Massachusetts, and also to examine in greater detail seasonal changes in patterns of community structure and species composition at one of the sedimentary environments. This study is presented to provide a context for a more detailed examination of methods of resource allocation in deposit-feeding faunal assemblages and micro-dispersion patterns of surface-feeding polychaete annelids.

[1] Present address: Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543.

MATERIALS AND METHODS

Barnstable Harbor, located on the northern shore of Cape Cod, is a shallow tidal embayment about 5.5 km long and 1.2 km wide. Over the past several decades a relatively large amount of research has been directed towards various aspects of the marsh ecology (see Redfield, 1972, for a partial list of references and an excellent description of the general development of the marsh system). The mean tidal range is about 2.9 m and approximately 60% of the tidal flats, where this study took place, are exposed at low tide (Ayers, 1959).

The physical environment of the region is typical of intertidal regions along the southern New England coast of North America. Water temperatures range from about 20° C during July to September to about 0–1° C during December to February. Sediment temperatures range from about 30° C in August to 1–2° C in December to February. The winter of 1974–1975 was unusually mild, and accumulation of ice on the flats was never observed. Ice buildup on the flats normally occurs from January to February (Green and Hobson, 1970; personal observations in the winter of 1975–1976). Ayers (1959) reports that salinity near the present study area varies between 29.6 to 31.7‰, with very little freshwater drainage in the harbor.
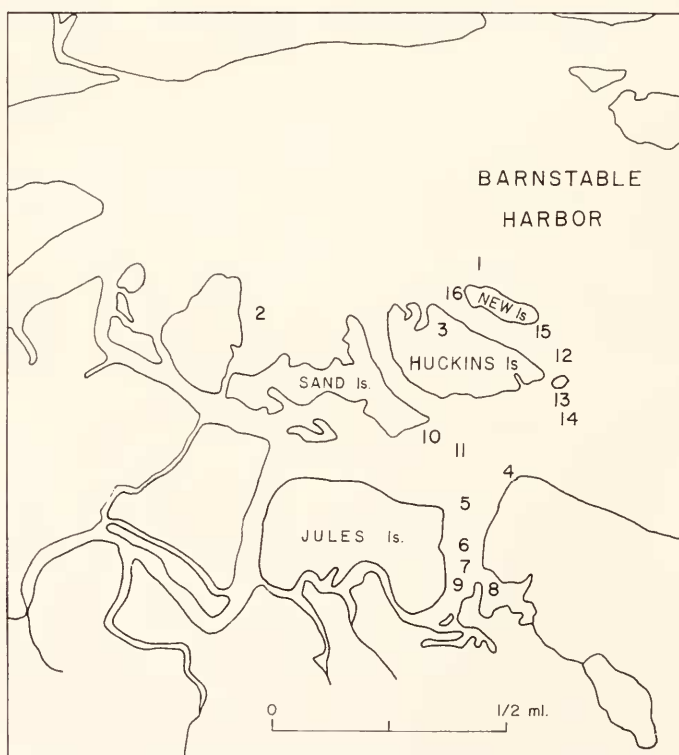

FIGURE 1. Map of western Barnstable Harbor, Massachusetts, indicating sampling localities.

The currents of Barnstable Harbor are controlled almost exclusively by the tides. Due to the large tidal range, strong currents occur in the harbor. Both Ayers (1959) and Sanders, Goudsmit, Mills, and Hampson (1962) have measured the currents at different regions within the harbor and found maximums from 30–80 cm/sec occurring during flood tides. The strongest currents occur just before the time of maximum ebb tide. The flats within the harbor, however, are not greatly affected by the strong currents, since they are always exposed before the time of maximum ebb current.

Changes in sediment accretion and erosion were monitored over a yearly period at stations 1 and 2 (Fig. 1). Results indicate minimal changes in the level of substratum at these localities during a 15 month period (on the order of 1–3 cm). Maximum sediment fluctuation occurred in the spring. Larger amounts of sediment movement were common, however, in the tidal creeks and areas closer to the mouth of the harbor.

Sixteen preliminary stations were sampled in the western portion of the intertidal sand and mud flats in June–July 1974. Faunal data collected from these stations were used to help in delimiting the general characteristics of the various macrofaunal assemblages of this region. One station was chosen from the initial sampling program for more detailed long-term sampling.

Samples were collected at low tide with a small hand held core 12.5 cm in diameter. The core was gently pushed into the substrate to a depth of 17–20 cm and removed with a shovel. The location of sampling sites at each station was determined by random sampling coordinates. Samples were brought to the laboratory and gently washed through a 250 μm mesh screen. The residues were preserved in 70% alcohol, sorted under a dissecting microscope and the organisms encountered were identified to species.

A small core (3.5 cm diameter) was used to sample surface sediment for substrate analysis. Sediment size-distributions were determined for each sample using standard wet-sieving analysis and mean particle size, and sorting coefficients were graphically determined from formulae of Folk (1966). The percentage of oxidizable organic carbon was estimated by the Walkley-Black wet oxidation method (Morgans, 1956).

Faunal data were subjected to classification and cluster analysis in an attempt to delimit community structure, species composition and seasonal community dynamics of the benthic macrofauna. This type of analysis has received extensive attention in marine community studies (*e.g.,* Lie, and Kelley, 1970; Stephenson and Lance, 1970; Hughes and Thomas, 1971; Stephenson, Williams and Cook, 1972; Boesch, 1973), and these authors have outlined the various methods.

In this study, the per cent similarity coefficient (a derivative of the Czekanowski similarity coefficient) was used. Stephenson *et al.* (1972) have briefly reviewed the characteristics of the different classification measures. The per cent similarity measure tends to be biased toward the more dominant and ubiquitous species, so that rarer species contribute little to the index. Preliminary data analysis comparing the fanual data with and without dominant forms, however, revealed that the clusters were not appreciably altered.

Two clustering strategies were initially employed: first, the more common group-average or unweighted pair-group method; and secondly, the newer and

more popular flexible sorting strategy. Lance and Williams (1967) and Williams (1971) have reviewed the basic properties of the two strategies. After initial data processing, it was found that the group-average clustering technique yielded the more instructive classification. The "flexible" method is a strong sorting strategy (William, 1971) which increases the distance between groups as the number of elements which they contain increases. While this heightens differences between groups, it tends to divide these elements into groups that may obscure the important characteristics of individual systems. (Comparisons of the two clustering strategies are available upon request.)

Both normal and inverse classification analyses were used in the study. Normal analysis (sometimes called Q-analysis) treats samples as individuals, each being composed of a number of attributes—the various species from a given sample. Normal analysis is instructive in helping to ascertain community structure and to infer specific ecologic conditions between sampling stations from the relative distributions of the species. Inverse classification (termed R-analysis) is based on species as individuals, each of which is characterized by its relative abundance in the various samples. This type of analysis is commonly used to reveal species groups within particular habitats.

Shannon's formula (Shannon and Weaver, 1963) expressed as: $H' = -\Sigma p_1 \log_2 p_i$, where p_i is the proportion of individuals belonging to the ith species, was used to estimate species diversity. Evenness, the distribution of the individuals among the various species, was computed as: $J' = H'/\log_2 s$, where s is the number of species in the sample (Pielou, 1966).

RESULTS

Sediments

A summary of the sedimentary features of the sampling localities is given in Table I. Four distinctive substrate types are evident: sandy sediment (stations 10–16), muddy-sand sediment (stations 1–2), muddy sediment (stations 3 and 5–9), and gravel-sand sediment (station 4).

The muddy stations are all located in slightly higher and more protected areas of the marsh and are relatively free from tidal motion. These sediments are characterized by both high silt-clay fractions and organic carbon content. Dead and decaying fragments of *Spartina alterniflora* are commonly found throughout these sediments.

The sandy stations can be further subdivided into two categories: fine (stations 12–14) and coarse (stations 10, 11, 15, 16) sand. Coarser sand is generally found closer to the tidal channels. The sands in these areas are moved freely by tidal currents, and the surface is commonly marked by sand ripples indicating sediment instability. The finer sand stations are further from the channels where current velocities are lower. These sediments are generally well-sorted and contain low percentages of organic carbon.

The very large sand flats north of New and Sand Islands (Fig. 1) are composed of well-sorted muddy-sands. These areas are more protected from current flow across the flats and any surficial ripple marks are normally the result of wave action. These sandy flats have slightly higher amounts of organic carbon

TABLE I

Sedimentary and trophic group parameters from the sampling stations at Barnstable Harbor (see Figure 1 for station locations).

Station number	Per cent silt-clay	Mean phi	Phi of sorting	Per cent carbon	Deposit-feeders*		Suspension-feeders*	
					Number species	Number/ m²(× 10³)	Number species	Number/ m²(× 10³)
1	11.9	2.48	0.18	0.48	19	45.7	2	1.30
2	20.9	2.47	0.30	0.78	12	39.0	0	—
3	91.0	4.09	0.40	1.52	3	52.2	0	—
4	1.3	0.53	0.83	0.37	12	6.3	1	0.08
5	48.6	3.10	0.33	0.57	15	33.3	0	—
6	34.2	3.00	0.33	0.66	9	18.7	0	—
7	88.7	4.22	0.45	1.49	6	35.8	0	—
8	87.6	4.10	0.38	1.54	11	21.1	0	—
9	80.4	3.81	0.37	1.35	11	23.5	0	—
10	4.1	1.90	0.35	0.10	8	2.4	3	2.00
11	2.5	1.78	0.40	0.07	4	0.9	1	0.20
12	11.4	2.15	0.48	0.32	17	30.3	2	104.90
13	7.9	2.13	0.45	0.33	9	11.9	3	44.80
14	7.5	2.05	0.43	0.31	9	4.5	2	192.90
15	2.1	1.47	0.38	0.22	7	6.5	2	28.20
16	2.6	1.60	0.32	0.09	13	8.2	1	0.08

* Feeding types determined from examination of gut contents, Sanders *et al.* (1962) and Barnes (1964).

and silt-clay fractions when compared to the sand areas. Monthly sediment samples at station 1 indicated no significant temporal change in mean grain size or sorting coefficient according to analysis of variance ($P > 0.05$).

The one station located on the south shore of the harbor consists of gravel, sand, and clay, all thought to be derived from erosion of the upland (Redfield, 1972). This sediment is very poorly sorted, with low organic carbon content. The presence of patches of scattered stones and gravel characterizes this very heterogeneous substrate.

General community description and species composition

Table II lists the macrofaunal species occurring in 64 core samples obtained from the preliminary sampling of 16 stations in Barnstable Harbor. Of the 47 species found in the survey, the majority were polychaetes (29 species), crustaceans (9 species) and molluscs (6 species). Individual replicate samples taken at each locality were not lumped together for use in the classification analysis so as to obtain an idea of within-habitat sampling variability. The results of the inverse classification analysis used to delimit species groups, however, are based only on those species which occurred more than five times in the survey. Species eliminated from the analysis include ten which occurred once, five which occurred twice, and only one which occurred three times.

Normal analysis. Figure 2 indicates that the samples are clustered into five major groups. Group A is composed of stations 12–15 containing clean, well-sorted sands with a low silt-clay fraction (2–5%). Group B, composed of samples

TABLE II

Macrobenthic species sampled at Barnstable Harbor, June–July, 1974.

Identification number	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Polychaeta																	
1	Streblospio benedicti	X	X	X	X	X	X	X	X	X	X		X	X	X		X
2	Eteone heteropoda	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
3	Lumbrinereis tenuis	X	X			X	X		X	X	X	X		X		X		X
4	Capitella capitata	X		X	X		X		X				X				
5	Glycera dibranchiata									X							
6	Polydora ligni			X	X	X											
7	Phyllodoce mucosa	X	X						X				X				
8	Heteromastus filiformis	X	X	X	X	X	X	X	X	X	X	X	X				
9	Scolecolepides viridis			X		X											
10	Scoloplos acutus	X				X						X	X	X	X	X	X
11	Spio setosa	X	X		X	X								X			
12	Scoloplos robustus						X	X									
13	Clymenella torquata					X			X								
14	Nereis arenaceodonta	X	X			X			X	X			X				X
15	Pectinaria gouldii	X	X		X	X	X										
16	Scolelepis squamata	X	X										X				X
17	Tharyx sp.	X	X		X								X				X
18	Nephtys picta	X															
19	Syllides verrilli	X	X			X	X	X	X	X	X		X	X	X		X
20	Spiophanes bombyx	X	X							X	X	X	X		X		X
21	Prionospio heterobranchia	X			X					X			X				
22	Paraonis fulgens																X
23	Aricidea jeffreysii	X															
24	Eteone longa													X		X	
25	Nereis virens				X					X							
26	Nephtys caeca										X						X
27	Amphitrite ornata					X											
28	Pygospio elegans										X			X	X	X	
29	Chaetozone sp.															X	
Mollusca																	
30	Hydrobia sp.	X											X	X	X	X	
31	Nassarius obsoletus	X		X		X			X				X				
32	Gemma gemma	X									X		X	X	X	X	
33	Mya arenaria	X			X						X	X	X	X			X
34	Retusa canaliculata	X	X														
35	Polynices duplicatus	X															
Crustacea																	
36	Diastylis polita													X		X	
37	Ampelisca abdita													X			
38	Oxyurostylis smithi	X															
39	Edothea triloba	X				X											
40	Crangon septemspinosus								X	X							
41	Corophium insidiosum												X				
42	Gammarus sp.												X				
43	Unicola irrorata		X								X						
44	Ampithoe rubricata					X	X		X								
Hemichordata																	
45	Saccoglossus kowalewskii																X
Oligochaeta																	
46	Phallodrilus monosperma-thecus												X	X		X	
47	Monophylephorus irroratus				X												

collected from stations 10, 11, and 16, is also a clean sand environment. These sediments, however, are coarser-grained with a smaller silt-clay fraction (2–3%). Group C contains the muddy sediment localities (stations 3 and 5–9) of Jules Island and Huckins Island. The major sedimentary features of these stations include high quantities of silt-clay (10–70%), small median grain size and high organic carbon content. The muddy-sand stations (1 and 2) fall into Group D. While sation 1 is more characteristic of a sandy sediment type, the larger silt-clay fraction makes it more similar to station 2 in sedimentary composition. Finally, Group E contains the very poorly sorted gravely-mud station.

Inverse analysis. The 32 species found at the various localities in Barnstable Harbor were divided into 10 groups (Fig. 3) by the inverse classification analysis.

Groups 1, 3, 5, and 7 are comprised of species which characteristically occur in clean sand areas. While normal classification analysis divided the sandy stations into two separate groups, fine and coarse sand, species groups generated by the inverse analysis indicate that degree of within-habitat species fidelity is low. About 39% of the species in these groups are found in both coarse and fine sands—the most striking visible difference being the presence of very large numbers of the small venerid bivalve *Gemma gemma* in the fine sands.

Group 4 is composed of the most ubiquitous and numerically most important species of Barnstable Harbor. *Streblospio benedicti, Eteone heteropoda,* and *Heteromastus filiformis* occur at each sediment type sampled. At sandy-mud and mud stations, *S. benedicti* and *E. heteropoda* were always ranked as the first and second most dominant species, respectively.

Groups 8 and 10 consist of species normally associated with sandy-mud and mud stations. Although normal classification analysis separated these two sediment types into discrete groups, the inverse analysis showed that between habitat species co-occurrence is high. Only two species, *Scoleocolepides viridis* and *Scoloplos robustus,* in these two groups were restricted to just one sediment type.

Group 9 consists of two species which are largely restricted to station 4, the most hetrogeneous substrate type. While the large nereid polychaete, *Nereis virens,* was also found at station 9, its greatest abundances occurred at station 4. The oligochaete, *Monophylephorus irroratus,* was never found to occur at any of the other 15 stations sampled.

Groups 2 and 6 contain just one species each. *Ampithoe rubricata,* a small amphipod, and the epifaunal tectibranch, *Retusa canaliculata,* were found in the muddy-sand stations 1 and 2. Both species were relatively rare in abundance.

In summary, inverse classification analysis produced four basic species groups: sandy faunal groups composed of species inhabiting both coarse and fine sand sub-
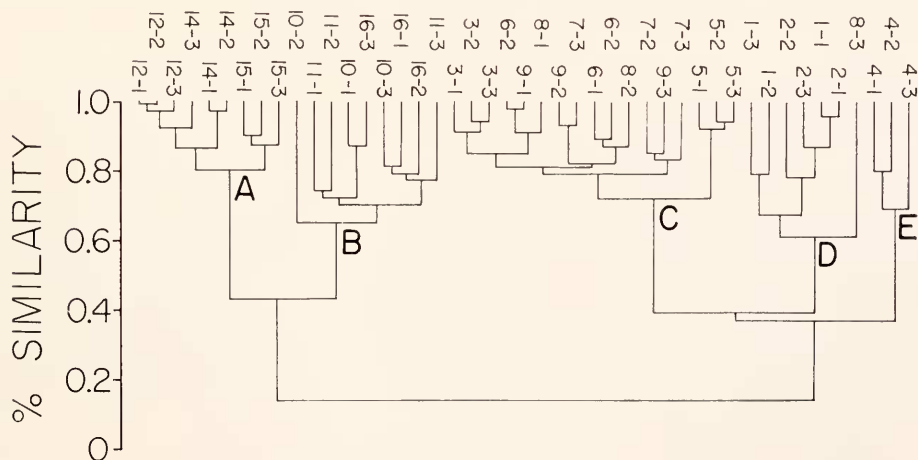

FIGURE 2. Dendrogram resulting from normal classification analysis of 16 sampling localities at Barnstable Harbor. First characters indicate sampling station (see Fig. 1); last digit indicates sample number.
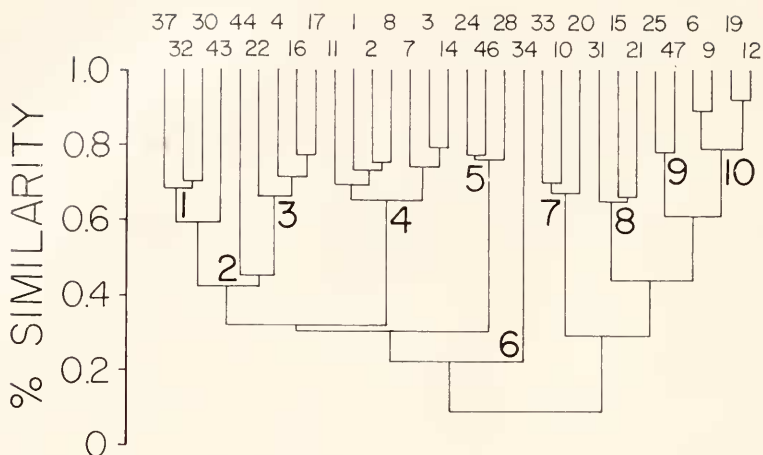
FIGURE 3. Dendrogram resulting from inverse clustering of species at the sampling stations. Species are indicated by code numbers (see Table II).

strata; ubiquitous forms characterizing the dominant faunal components of Barnstable Harbor; muddy and sandy-mud species; and single species groups which are both rare and restricted to a single sediment type.

Animal-sediment relationships. While more detailed information will be presented in a later paper (in preparation) on the feeding ecologies of the dominant benthic macrofauna, it is interesting to examine the general trophic-group sediment-type relationships found at Barnstable Harbor. Table I lists information regarding the abundance and species number of the two major trophic groups: suspension- and deposit-feeders. The majority of the benthic fauna at Barnstable Harbor are comprised of deposit-feeding species. *Mya arenaria* and *Gemma gemma* are the two most abundant suspension-feeding organisms. These forms dominate at stations 12–15 which contain well-sorted, relatively fine sands with low silt-clay and organic carbon values. *G. gemma* comprises over 99% of the abundance of the suspension-feeding forms at these stations. *G. gemma* is widely distributed and abundant in fine sands. In coarser sand localities, where surface rippling becomes increasingly pronounced, the bivalve density is low. Sediment instability resulting from waves and currents readily move this small bivalve and are probably responsible in determining its distributional pattern. *M. arenaria* is much rarer and comprises less than 1% of the total number of suspension-feeders at the sampling stations. Bradley and Cooke (1959) and Sanders *et al.* (1962) have hypothesized that high density populations of *G. gemma* inhibit larval settling of *M. arenaria*. Deposit-feeders predominate at stations 1–9 where both organic matter and silt-clay fractions are the highest. The coarse sand, ripple-marked stations (10, 11, 16) show reduced numbers and species diversity of both trophic groups.

Seasonal changes in community structure and species composition

Station 1 was sampled at approximately monthly intervals for a period of 19 months to obtain information on the degree of temporal fluctuation in both community structure and species composition.

While the basic unit of structure in any natural community is the individual, examination of the total species complement of a particular assemblage or community of organisms can provide insight into distinguishing temporal changes of community organization. Figure 4 summarizes three such measures of community structure at station 1: species diversity (H′), evenness (J′), and
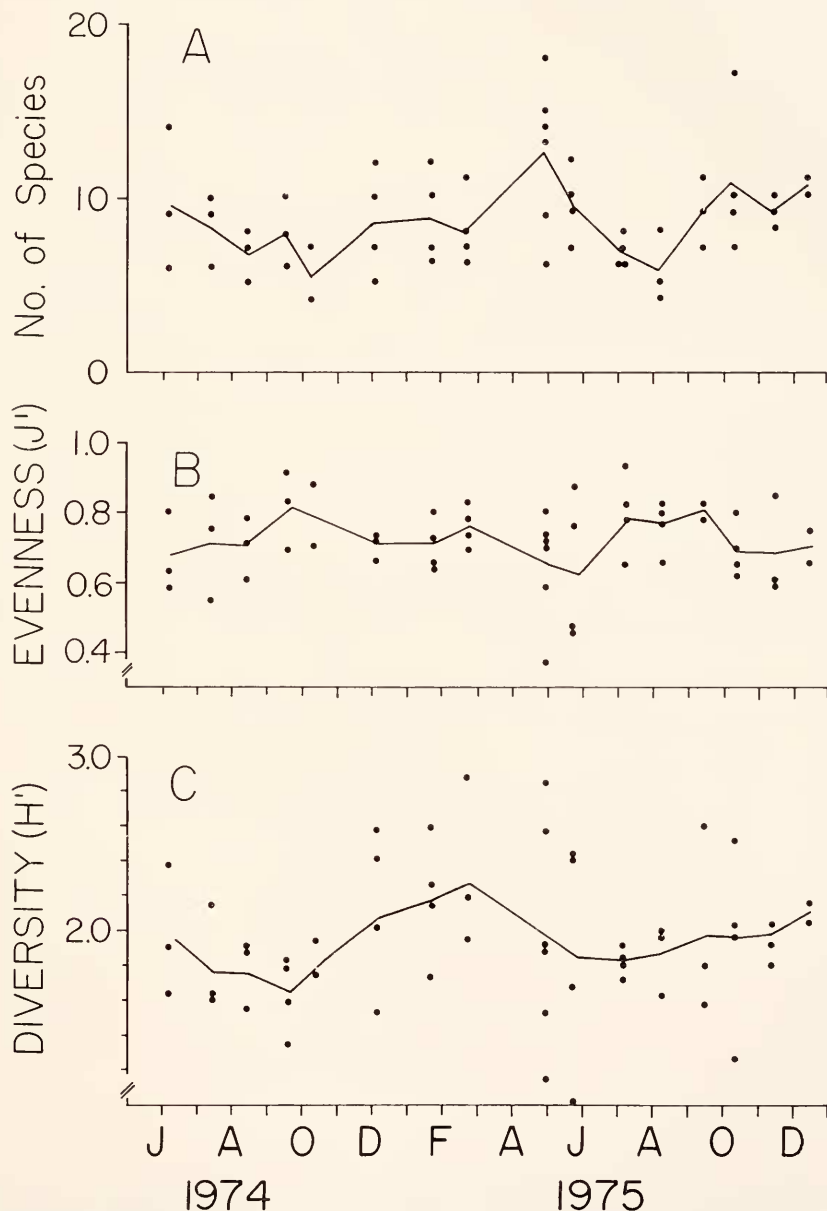

FIGURE 4. Temporal changes in number of species/245 cm² (A); evenness (B); and species diversity (C) at station 1.

number of species. While all three measures show some temporal variation throughout the sampling period, they did not vary significantly according to the results of one-way analysis of variance ($P > 0.05$). It should be noted, however, that indices similar to the ones used are not sensitive to subtle changes in species composition. In particular, Shannon's index H' is biased toward the more dominant species and the rarer members contribute little to the measure. Also, these measures do not provide any information regarding what species are actually characteristic of a given sample(s) during different periods of the year. For these reasons classification analysis was adopted to examine the degree of temporal partitioning of samples collected throughout the year and to elucidate changes in species composition at station 1.

Normal analysis. Figure 5 presents the results of normal classification analysis of 46 samples collected from June 1974 to December 1975. Generally the major groupings derived from this procedure are subdivided by seasonal similarity and can be grouped into four clusters. Group A is largely a "winter" cluster comprising samples collected from October to January. Group B contains collections from March–May and can be regarded as a "spring" cluster. Groups C and D can be classified as "summer" and "fall" groups, respectively, though the level of separation of these two clusters is higher than found in Groups A and B.

It is evident that there is a certain degree of sample overlap between the clusters, indicating spatial variation in species abundance and composition of individual samples. Group B (spring cluster) contains one sample collected during the fall (October, 1975). Groups C and D have the greatest amount of sample overlap between clusters; each contain two samples that are not similar on a seasonal basis with other samples in the group. In all cases, upon examination of the original data matrix these samples were characterized by the absence of the rarer species which normally had occurred at other times of the year in the other samples.
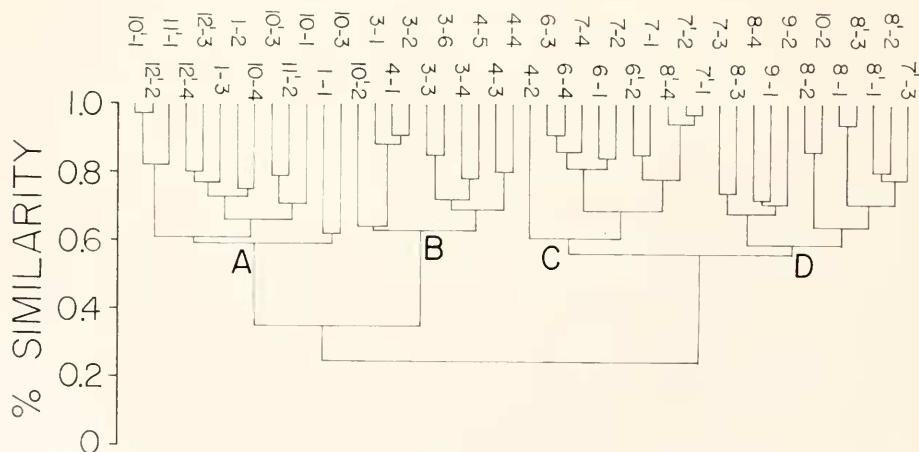

FIGURE 5. Dendrogram resulting from normal analysis of sampling station 1 from June, 1974 to December, 1975. First characters indicate the month sample was collected (prime numbers = 1975). Last number indicates sample number.

Inverse analysis. Species that occurred less than five times during the sampling program were excluded from the inverse analysis. Those species eliminated included six species that occurred only once, two forms occurring twice, and one species occurring three times. Twenty-one species were included in the analysis.

Again, four basic seasonal species groupings are evident at station 1 (Fig. 6). As would be expected, individual clusters are composed of species whose seasonal peak population abundance levels coincide with one another. Table III provides information on the time of the highest numerical abundance coupled with data on the reproductive activities of each species included in the analysis. Data on reproductive behavior of each species were compiled from published sources and personal observations. Unfortunately, some of these data are based on limited observations. In general, however, there is a close concordance between the peak population abundance levels of species and their periods of reproductive activity. In most instances there is a one to two month delay between the observation of reproductively active adults and the appearance of the new year class into the benthic population. This time lag may either be associated with the planktonic larval phase exhibited by most of the species in this study or may be the result of sampling bias. Although the use of smaller meshed screens proved impractical in this study, they may provide a more exact time scale of larvae entering the benthic populations.

Species group 1 is composed of organisms whose recruitment generally occurs in the spring and early summer months. This group contains those faunal elements which are normally the dominant components of this station. Group 2 contains species that are generally most abundant during the warmest fall months of the year. Four species of polychaetes and one species of amphipod, whose peak abundances occur in the coldest months of the year, comprise Group 3. Group 4 contains six species whose recruitment of individuals into benthic populations occurs during the late summer months of July–September.

Population characteristics of the dominant species. Figure 7 shows a summary of the seasonal changes in the population abundance of five of the most
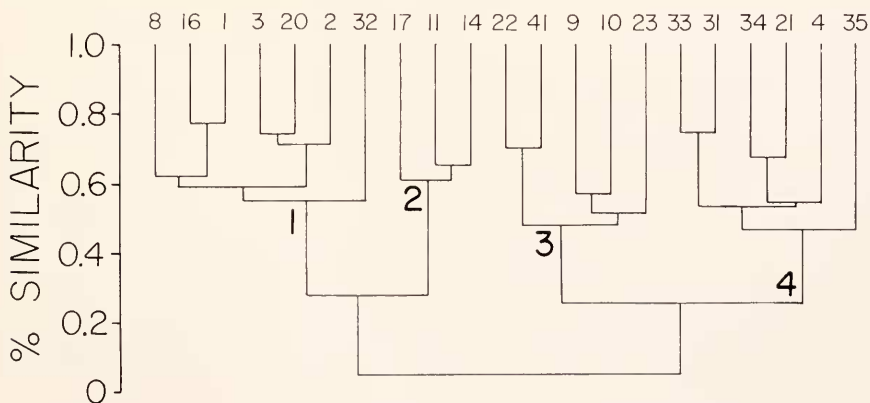

FIGURE 6. Dendrogram indicating seasonal species groups at station 1 using inverse classification analysis. Species are indicated by code numbers (see Table II).

numerically important species at station 1. *S. benedicti,* generally the most abundant and ubiquitous polychaete found in Barnstable Harbor, comprises 20–70% of the total fauna at station 1. Abundance patterns of this small spionid are highly seasonal with greatest numbers occurring in early spring. Rapid decreases occurred in the summer months in both 1974 and 1975. Much of this decline is attributable to the loss of larger individuals from the population. Size-frequency distributions of this organism are uni-modal, characteristic of annual species. The new-year class enters the population in June and continues to grow throughout the winter and following spring (unpublished). Watling (1975) and Jones (1961) found similar seasonal abundance patterns of *S. benedicti* in Delaware and southern California populations, respectively. Watling (1975) listed size data indicating the annual nature of this species.

E. heteropoda and *H. filiformis* also appear to be relatively short-lived. Size-frequency distributions of *E. heteropoda* indicate three separate modes, suggesting at least three year classes are found in the population. The 0-year class enters the population in July and continues to grow throughout the year. The population abundance of *H. filiformis,* on the other hand, was quite stable throughout the sampling program. Changes in the size-frequency distributions of this species indicate the 0-year class enters the benthic population in July–August. The size distributions also indicate two distinct size classes, suggesting first and second year groups. Buchanan and Warwick (1974) found a similar life history pattern in *H. filiformis;* however, 0-year groups appeared in January on the coast of Britain.
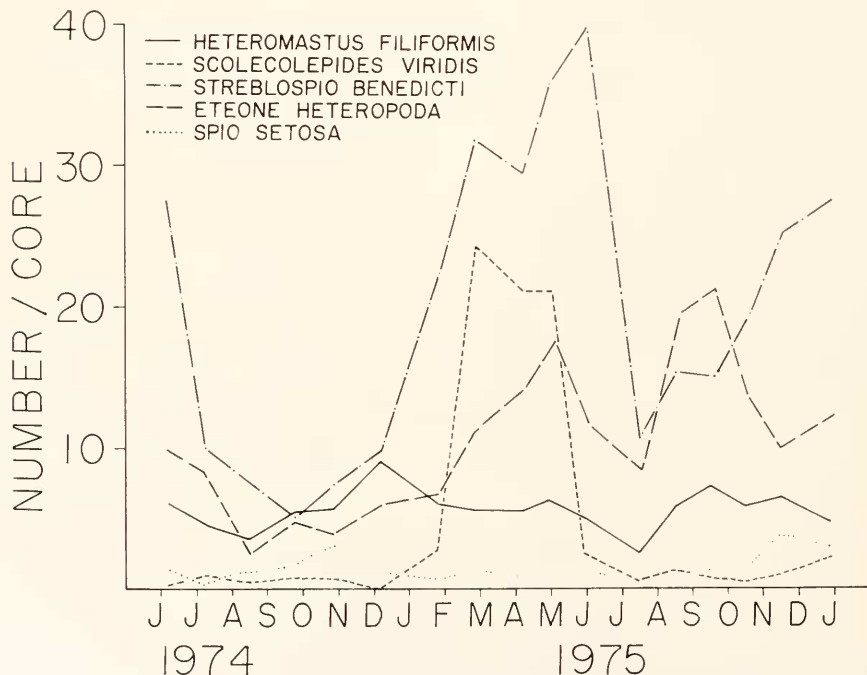

FIGURE 7. Estimated abundance (number per 245 cm²) of the five most common macrobenthic species at station 1 from June 1974 to December, 1975.

TABLE III

Seasonal species groups at Barnstable Harbor, time of peak population abundance, reproductive activity, and geographic range along the eastern coast of North America.

Group	Species	Peak Abundance	Reproductive activity*	Range**
1	*Streblospio benedicti*	June	June–Oct.	C
	Heteromastus filiformis	July–Aug.	June–July	C
	Scolelepis squamata	April–June	Mar.–June	C
	Lumbrinereis tenuis	May–June	June	C
	Spiophanes bombyx	May–June	June–Aug.	C
	Eteone heteropoda	June–July	June (?)	C
	Gemma gemma	May–June	May–Aug.	C
2	*Tharyx* sp.	Sept.–Oct.		V
	Nereis arenaceodonta	Aug.–Oct.	Aug.	V
	Spio setosa	Sept.	Oct.–Feb.	V
3	*Scolecolepides viridis*	Feb.–May	Oct.–Nov.	N
	Scoloplos acutus	Feb.–April	Feb.–July	N
	Aricidea jeffreysii	April–May	July	C
	Paraonis fulgens	Jan.–Feb.		N
	Corophium insidiosum	April–May	April–Aug.	N
4	*Mya arenaria*	Sept.–Oct.	Sept.–Oct.	C
	Nassarius obsoletus	Aug.–Sept.	June–July	C
	Retusa canaliculata	Aug.–Sept.	June–Aug.	C
	Prionospio heterobranchia	July	April–July (?)	V
	Capitella capitata	July–Aug.	April–Nov.	C
	Polinices duplicatus	Aug.–Sept.		V

* Information obtained from: personal observations; Simon and Brander, 1967; Pettibone, 1963; George, 1966; Dean, 1965; Grassle and Grassle, 1974; Scheltema, 1962; Turner, 1951; Grant, 1965.

** Biogeographic range of species: C = generally ranging along entire North American coast; V = generally occurring from Massachusetts to Florida; N = normally ranging from Maine to Massachusetts. Information from: Pettibone, 1963; Day, 1973; Foster, 1971; Abbott, 1954; Bousfield, 1973.

The large spionid, *Spio setosa,* showed two separate population abundance peaks, one which occurred in November and a slightly larger one which occurred in May (Fig. 7). *S. setosa* appears to exhibit two reproductive periods: first, a spring period in which eggs are laid in female tubes and develop into benthic larvae; and secondly, a fall period in which pelagic larvae are abundant (Simon, 1967, 1968). The two peaks in abundance found at station 1 probably reflect the two recruitment periods.

Figure 7 shows that *Scolecolepides viridis* is most abundant during February–May. During the remainder of the year, a small and relatively stable population level is found at station 1. George (1966) reports that *S. viridis* spawns from October–November in Nova Scotia, Canada, waters, and reproductive activity appears to be inversely correlated with increases in water temperature.

DISCUSSION

As with other benthic studies, sedimentary parameters appear to be influencing general trophic and species composition of the macrobenthos at Barnstable Harbor.

The work of Sanders (1958, 1960) has brought into focus the importance of sedi-
mentary features that influence the distribution of suspension- and deposit-feeding
benthos.   From examination of the theoretical properties of sediment dynamics,
Sanders postulated a value of 0.18 mm as the optimal grain size for supporting
suspension-feeders.   He also suggested that high silt-clay fractions in sediments
(relating to greater amounts of food) helped to explain the presence of the
deposit-feeding benthos.   Though these predictions have been successfully tested
in the majority of subtidal surveys (but see McNulty, Work and Moore, 1962),
they show inconsistencies when applied to intertidal studies (Sanders, *et al.*,
1962; Bloom, *et al.*, 1972).   Examination of Table I indicates that areas dominated
by suspension-feeders (though they normally comprise 1–2 species) have an average
median grain size of 0.28 mm, larger than Sanders' predicted value.   The impor-
tance of high silt-clay fractions influencing the distribution and abundance of deposit-
feeders, however, is very evident in this table.

The survey of Sanders (1958) also suggested that the distribution of suspension-feeders is
greatly effected by sediment instability (median grain size greater than 0.18 mm).
Data from most coarse sand stations (10, 11, and 15) at Barnstable Harbor indicate
that the abundance of both deposit- and suspension-feeders is sharply reduced.
These stations are characterized by pronounced surficial ripple marks, evidence of
sediment instability.   This instability coupled with low amounts of organic carbon
and silt-clay fractions explain the reduced abundances of both trophic groups in
these areas.

The survey of Sanders *et al.* (1962) of five locations on or near Huckins Island,
Barnstable Harbor, found that two sediment types (muds and stable sands)
were dominated by deposit-feeding trophic *biomass* at four of the stations and did
not fit the predictions stated above.   Re-examination of the data, however, indicates
that the *numerical abundance* of the two trophic groups tends to be correlated
with amounts of silt-clay.   Stations A and C (Sanders *et al.*, 1962) dominated by
G. gemma, have the lowest amount of silt-clay.   Deposit-feeders dominate at those
stations with higher percentages of silt-clay.   Median grain size relationships,
however, show no significant trends in predicting benthic trophic structure.   The
reasons for the discrepancies in the two sets of data are unknown.   Comparisons
of both sedimentary parameters and rank order abundance of the macrobenthos
indicate major long-term (over 15 years) changes at all localities have taken place.

While examination of temporal changes at one sedimentary type at Barnstable
Harbor revealed distinct seasonal change in species composition, no patterns in
species diversity, evenness, or number of species per sampling date occurred.
Normal classification analysis indicated seasonal clustering of samples collected over
a 19 month period.   Clusters, though exhibiting overlapping elements between these
groups, show repeatable yearly trends characteristic of habitats in a dynamic
"equilibrium," not successional state.   The majority of benthic species at Barnstable
Harbor exhibit distinctive seasonal fluctuations in numerical abundance, and most
appear to be rather short-lived (1–3 years).   Due to the dynamic temporal
nature of recruitment and mortality patterns characteristic of short-lived species,
it is not surprising that one finds seasonal species specific population trends at
station 1.   Inverse classification analysis clustered species into four groups,
generally corresponding to seasonal population abundance peaks and periods of
reproductive activity.

The majority of studies examining mechanisms influencing seasonal abundance patterns of species attribute such change to regular or systematic change in resource quality and abundance (Fretwell, 1972). Since the benthic fauna inhabiting the intertidal sand and mud flats are greatly affected by sedimentary characteristics, seasonal changes in sediment could promote population change. As mentioned, however, there were no significant changes in sediment size composition over a 19 month period. Thorson (1957) and Muus (1967) have suggested that settling patterns of many benthic organisms coincide with food availability. Seasonal fluctuations in planktonic organisms are common in this area of New England (Lillick, 1937) and could affect benthic organisms feeding upon them. However, most of the species occurring at Barnstable Harbor are infaunal deposit-feeders which obtain the majority of their nutrition directly from sediments. Temporal change in sediment food supply (measured as total organic carbon and potential food particulate matter) remained relatively stable throughout the year at most of the sampling stations (Whitlatch, in preparation). The effects of well-buffered seasonal food supplies influencing population characteristics of deposit-feeders has been reviewed by Levinton (1972).

Temperature is commonly considered to be the most important single factor influencing the distribution and reproductive activities of marine invertebrates (Thorson, 1946). Temperature fluctuations at Barnstable Harbor show marked temporal variation and are repeatable from year to year; two features that could affect observed repeatable seasonal clustering patterns of species groups. While temperature may provide a seasonal cue for community change, it does not totally explain why some groups of organisms are commonly found in the winter months while others are restricted to the summer months.

A partial explanation of the occurrence of seasonal species groups can be obtained from a closer examination of the latitudinal distributional patterns of many of the species. Cape Cod, Massachusetts, has long been considered a zoogeographic boundary between the southern part of the cold-temperate Nova Scotian faunal province and the northern portion of the mild-temperate Virginian faunal province (see Hazel, 1970, for a historical review) due to differences in summer water temperature found on the north and south sides of the Cape (Schopf, 1967). Several studies of offshore benthic organisms have shown distinct faunal elements characteristic of these two areas (Parker, 1948; Peterson, 1964; Schopf, 1965; Hazel, 1970). Barnstable Harbor is somewhat unique in that it contains faunal elements common to both zoogeographic provinces, coupled with a group of species found to occur throughout the entire eastern coast of North America.

Distributional ranges of the various species, summarized in Table III, indicate several distinct trends when related to seasonal temperature fluctuations. The Virginian components are generally found at their greatest abundance during the warmest months of the year (August–October), while the Nova Scotian elements are most common during the coldest temperature months of the year (January–April). The cosmopolitan forms, comprising the largest group of species, generally are most abundant during early spring and summer months. The Nova Scotian and Virginian faunal elements do not seem to be geographically limited by winter temperature since shallow water temperatures are about the same on both sides of the Cape (Schroeder, 1966; Schopf, 1967). Potentially southward migrating forms are limited by summer temperatures too high for adult survival. North-

ward migrating species are limited by summer temperatures that never are high enough for reproductive activity to be initiated. Summer water temperatures at Barnstable Harbor are higher than surrounding Cape Cod Bay water due to the shallow nature of the area, explaining the occurrence of Virginian faunal components.

While the examination of faunal elements characteristic of the two zoogeographic provinces helped to shed light on mechanisms influencing some seasonal community change, other species may be responding to the effects of biological interactions (mainly competition and predation) from other species. Certain species of deposit-feeding polychaetes which overlap greatly in both food and space utilization are temporally segregated, thus reducing the possibility of competitive interactions in resource use (Whitlatch, in preparation). Also, common epifaunal predators at Barnstable Harbor (mainly *Fundulus heteroclitus* and *Nassarius obsoletus*) which are abundant during the summer-fall months, can exert disproportionate seasonal effects on infaunal populations and can alter the species dominance structure of soft-bottom communities (Schneider, 1976; Whitlatch, unpublished). Species reproducing during times of minimal predator activity could significantly reduce the effects of predation.

The degree to which seasonal clustering patterns at the various habitats in Barnstable Harbor persist for longer periods of time is unknown at present. Comparisons of the present study with other studies of Barnstable Harbor (Sanders, *et al.*, 1962; Mills, 1967) revealed major long-term changes in both sedimentary features and species structure at several localities during the summer months. While temperature appears to be one of the controlling mechanisms for initiating reproductive activity in most species, the exact timing of the appearance of larvae in benthic populations certainly is influenced by year-to-year fluctuations in temperature cycles characteristic of this area of New England. This unpredictable environmental variable will place constraints on the degree of long-term stability of the re-occurring seasonal species groups at Barnstable Harbor. Lie and Evans (1973) provide one of the few studies examining long-term (7 years) changes in species composition of various faunal assemblages in subtidal areas of Puget Sound, Washington. While they found relatively small species changes, Lie (1968) indicated that there was little fluctuation in environmental parameters (*e.g.*, temperature) in this area—a feature unlike Barnstable Harbor.

Seasonal changes in community structure have been noted in several subtidal surveys (*e.g.*, Tenore, 1972; Boesch, 1973) and several authors have recorded seasonal groups of particular organisms in subtidal areas (Levings, 1975; Muus, 1967; Bodiou and Chardy, 1973; Grassle and Smith, 1976). Environments characteristic of seasonal patterns of species composition are relatively unstable and "physically-controlled" (Sanders, 1968); namely, estuarine or intertidal and shallow-subtidal habitats where both the probability of environmental disturbance and magnitude of seasonal fluctuations in environmental parameters are more likely to affect biological changes. The distinct seasonal clusterings of species at Barnstable Harbor, while an important characteristic of the area, may be even more pronounced than other areas owing to its somewhat unique geographic position and hydrographic conditions which have the potential of magnifying the effects of temporal community change.

In a review of the community concept and its validity when applied to marine benthic ecology, Stephenson (1973) pointed out the lack of the addition of a *temporal* component to most community definitions. While most benthic ecologists view communities as loosely organized suites of re-occurring species, they fail to recognize the dynamic temporal nature of the organization of the component members. This failure can be largely attributed to the short-term ("one-shot") nature of sampling in the vast majority of sampling programs. To better understand the nature of communities, physical and biological parameters which influence them, and their persistence or stability, it is important to gain knowledge of temporal changes in community structure. Understanding these patterns will provide further insight into the nature of the structure and evolution of marine soft-bottom biological systems.

Summary

1. A quantitative sampling survey of the benthic macrofauna inhabiting the intertidal sand and mud flats of Barnstable Harbor, Massachusetts, was conducted to describe general community structure and examine temporal changes in species composition.

2. Classification analysis delimited coarse and fine sand, mud, muddy-sand, and gravel-mud benthic species associations. The 32 species used in the inverse classification analysis were partitioned into 10 species groups, reflecting spatial distributional patterns. Many of the species were both dominant and ubiquitous, masking discrete species groupings.

3. The majority of macrobenthos at Barnstable Harbor were deposit-feeders which comprised more than 90% of all organisms sampled. The deposit-feeders normally dominate mud and muddy-sand sediments. Suspension-feeders were most abundant in fine sands. The relationship of sedimentary parameters affecting the distribution of both trophic groups proposed by Sanders is generally supported.

4. While no significant changes were evident in species diversity, evenness, or species number throughout a 19 month sampling period, classification analysis delimited seasonal clustering of both samples and species groupings. These patterns were repeatable over a two year period suggesting that dynamic "equilibrium," not successional change was occurring.

5. Seasonal clustering patterns of some species were related to the appearance of different zoogeographic faunal province elements. Typical warm-temperature Virginian components and cold-temperate Nova Scotian species were commonly found in late summer and winter, respectively.

LITERATURE CITED

ABBOTT, R. T., 1954. *American seashells.* D. Van Nostrand, Co., Princeton, 541 pp.

AYERS, J., 1959. The hydrography of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.,* 4: 448-462.

BARNES, R. D., 1974. *Invertebrate zoology.* W. B. Saunders, Co., Philadelphia, 870 pp.

BLOOM, S. A., J. L. SIMON, AND V. D. HUNTER, 1972. Animal-sediment relations and community analysis of a Florida estuary. *Mar. Biol.,* 13: 43-56.

BODIOU, J.-Y., AND P. CHARDY, 1973. Analyse en composantes principales du cycle annuel d'un peuplement de copepods harpactoides de sables fin infralittoraux de Banyuls-sur-Mer. *Mar. Biol.,* 20: 27-34.

BOESCH, D. F., 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. *Mar. Biol.,* 21: 226-244.

BOUSFIELD, E. L., 1973. *Shallow-water gammaridean Amphipoda of New England.* Cornell University Press, Ithaca, 312 pp.

BRADLEY, W. H., AND R. COOKE, 1959. Living and ancient populations of the clam *Gemma gemma* in a Maine coast tidal flat. *U. S. Fish. Wildl. Serv. Fish. Bull.,* 58: 304-334.

BUCHANAN, J. B., AND R. M. WARWICK, 1974. An estimation of benthic macrofauna production in the offshore mud of the Northumberland coast. *J. Mar. Biol. Assoc. U. K.,* 54: 304-334.

DAY, J. H., 1973. New polychaetes from Beaufort, with a key to all species recorded from North Carolina. *National Oceanic and Atmospheric Administration, Technical Report,* 375: 1-140.

DEAN, D., 1965. On the reproduction and larval development of *Streblospio benedicti* Webster. *Biol. Bull.,* 128: 67-76.

FOLK, R. L., 1966. A review of grain-size parameters. *Sedimentology,* 6: 3-26.

FOSTER, N. M., 1971. Spionidae (Polychaeta) of the Gulf of Mexico and the Caribbean Sea. *Fauna Curacao Other Carib. Islands,* 36: 1-183.

FRETWELL, S. D., 1972. *Populations in a seasonal environment.* Princeton University Press, Princeton, 317 pp.

GEORGE, J. D., 1966. Reproduction and early development of the spionid polychaete *Scolecolepides viridis* Verrill. *Biol. Bull.,* 130: 76-93.

GRANT, D. C., 1965. Specific diversity in the infauna of an intertidal sand community. Ph.D. Dissertation, *Yale University,* New Haven, Connecticut, 53 pp.

GRASSLE, J. F., AND J. P. GRASSLE, 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. *J. Mar. Res.,* 32: 253-284.

GRASSLE, J. F., AND W. SMITH, 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologia,* 25: 13-22.

GREEN, R. H., AND K. D. HOBSON, 1970. Spatial and temporal structure in a temperate intertidal community, with special emphasis on *Gemma gemma* (Pelecypoda: Mollusca). *Ecology,* 51: 999-1011.

HAZEL, J. E., 1970. Atlantic continental shelf and slope of the United States—Ostracode zoogeography in the southern Nova Scotia and northern Virginian faunal provinces. *U. S. Geol. Sur. Prof. Pap.,* 259E: 1-22.

HOLLAND, A. F., AND T. T. POLGAR, 1976. Seasonal changes in the structure of an intertidal community. *Mar. Biol.,* 37: 341-348.

HUGHES, R. N., AND M. L. H. THOMAS, 1971. The classification and ordination of shallow-water benthic samples from Prince Edward Island, Canada. *J. Exp. Mar. Biol. Ecol.,* 7: 1-39.

JOHNSON, R. G., 1970. Variations in diversity within benthic marine communities. *Am. Natur.,* 104: 285-300.

JONES, M. L., 1961. A quantitative evaluation of the benthic fauna off Point Richmond, California. *Univ. Calif. Publ. Zool.,* **67**: 219–320.

LANCE, G. N., AND W. T. WILLIAMS, 1967. A general theory of classificatory sorting strategies. I. Hierarchial systems. *Comput. J.,* **9**: 373–380.

LEVINGS, C. D., 1975. Analysis of temporal variation in the structure of a shallow-water benthic community in Nova Scotia. *Int. Rev. Ges. Hydrobiol.,* **55**: 449–469.

LEVINTON, J., 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. *Am. Natur.,* **106**: 472–486.

LIE, U., 1968. A quantitative study of benthic infauna in Puget Sound, Washington, U. S. A., in 1963–1964. *Fiskeridir. Skr. Ser. Havunders.,* **14**: 229–556.

LIE, U., AND R. A. EVANS, 1973. Long-term variability in the structure of subtidal benthic communities in Puget Sound, Washington, U. S. A. *Mar. Biol.,* **21**: 122–126.

LIE, U., AND J. C. KELLEY, 1970. Benthic infauna communities off the coast of Washington and in Puget Sound: identification and distribution of the communities. *J. Fish. Res. Board Can.,* **27**: 621–651.

LILLICK, L., 1937. Seasonal studies of the phytoplankton off Woods Hole, Massachusetts. *Biol. Bull.,* **73**: 488–503.

McNULTY, J. K., R. C. WORK, AND H. B. MOORE, 1962. Some relationships between the infauna of the level bottom and the sediment in South Florida. *Bull. Mar. Sci.,* **12**: 322–332.

MILLS, E. L., 1967. The biology of an Ampeliscid amphipod crustacean sibling species pair. *J. Fish. Res. Board Can.,* **24**: 305–355.

MORGANS, J. F. C., 1956. Notes on the analysis of shallow water soft substrata. *J. Anim. Ecol.,* **25**: 367–387.

MUUS, B. J., 1967. The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow beaches of the mesohaline zone. *Medd. Dan. Fisk. Havunders,* **5**: 1–316.

PARKER, F. W., 1948. Foraminifera of the continental shelf from the Gulf of Maine to Maryland. *Harvard Univ. Mus. Comp. Zool. Bull.,* **100**: 213–241.

PEARSON, T. H., 1971. The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. III. The effect on the benthic fauna of the introduction of pulp mill effluent. *J. Exp. Mar. Biol. Ecol.,* **6**: 211–233.

PETERSON, C. G. J., 1918. The sea bottom and its production of fish food. A survey of the work done in connection with the valuation of the Danish waters from 1883–1917. *Rep. Dan. Biol. Sta.,* **25**: 1–62.

PETERSON, K. W., 1964. Some preliminary results of a taxonomic study of the Hydrozoa of the Cape Cod area. *Biol. Bull.,* **127**: 384–385.

PETTIBONE, M. H., 1963. *Marine polychaete worms of the New England region. 1. Aphroditidae through Trochochaetidae.* Smithsonian Institution Museum of Natural History, Washington, D. C., 356 pp.

PIELOU, E. C., 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.,* **13**: 131–144.

REDFIELD, A. C., 1972. Development of a New England salt marsh. *Ecol. Monogr.,* **42**: 201–237.

SANDERS, H. L., 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.,* **3**: 245–258.

SANDERS, H. L., 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. *Limnol. Oceanogr.,* **5**: 138–153.

SANDERS, H. L., 1968. Marine benthic diversity: a comparative study. *Am. Natur.,* **102**: 243–282.

SANDERS, H. L., E. M. GOUDSMIT, E. L. MILLS, AND G. R. HAMPSON, 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.,* **7**: 63–79.

SCHELTEMA, R. S., 1962. Pelagic larvae of New England intertidal gastropods. I. *Nassarius obsoletus* and *Nassarius vibex.* *Trans. Am. Microsc. Soc.,* **8**: 1–12.

SCHNEIDER, D. C., 1976. The structural reorganization of a salt marsh community following a disturbance. *Master's Thesis, State University of New York,* Stony Brook, New York, 48 pp.

SCHOPF, T. J. M., 1965. Ectoproct (Bryozoa) distribution in the Atlantic continental shelf from Hudson Canyon to Nova Scotia. *Biol. Bull.,* **129**: 421–422.

SCHOPF, T. J. M., 1967. Bottom-water temperatures on the continental shelf off New England. *U. S. Geol. Sur. Prof. Pap.,* **575D**: 192–197.

SCHROEDER, E. H., 1966. Average surface temperatures of the western North Atlantic. *Bull. Mar. Sci.,* 16: 302–323.

SHANNON, C. E., AND W. WEAVER, 1963. *The mathematical theory of communication.* University of Illinois Press, Urbana, 117 pp.

SIMON, J. L., 1967. Reproduction and larval development of *Spio setosa* (Spionidae; Polychaeta). *Bull. Mar. Sci.,* **17**: 398–431.

SIMON, J. L., 1968. Occurrence of pelagic larvae in *Spio setosa* Verrill, 1873 (Polychaeta: Spionidae). *Biol. Bull.,* **134**: 503–515.

SIMON, J. L., AND K. M. BRANDER, 1967. Reproductive biology and larval systematics of Cape Cod polychaetous annelids. Pages 41–44 in *Systematics-ecology fifth annual report.* Marine Biological Laboratory, Woods Hole, Massachusetts.

STEPHENSON, W., 1973. The validity of the community concept in marine biology. *Proc. R. Soc. Queensl.,* **84**: 73–86.

STEPHENSON, W., AND G. N. LANCE, 1970. The macrobenthos of Moreton Bay. *Ecol. Monogr.,* **40**: 459–494.

STEPHENSON, W., W. T. WILLIAMS, AND S. COOK, 1972. Computer analysis of Peterson's original data on bottom communities. *Ecol. Monogr.,* **42**: 387–415.

TENORE, K. R., 1972. Macrobenthos of the Pamlico River estuary, North Carolina. *Ecol. Mongr.,* **42**: 51–69.

THORSON, G., 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Medd. Komm. Fisk. Havunders. Copenhagen Ser. Plankton,* **4**: 1–523.

THORSON, G., 1957. Bottom communities (sublittoral or shallow shelf). Pages 461–534, in J. W. Hedgpeth, Ed., *Treatise on marine ecology and paleoecology, Volume 1.* Geological Society of America Memoir 67, Waverly Press, Baltimore, 1296 pp.

TURNER, H. J., 1951. *Fourth report on investigation of the shellfisheries of Massachusetts.* Commonwealth of Massachusetts, Department of Conservation, Division of Marine Fisheries, Boston, Massachusetts, 21 pp.

WATLING, L., 1975. Analysis of structural variations in a shallow water estuarine deposit-feeding community. *J. Exp. Mar. Biol. Ecol.,* **19**: 275–313.

WILLIAMS, W. T., 1971. Principles of clustering. *Annu. Rev. Ecol. Syst.,* **2**: 303–326.